HANDEDNESS, WITH SPECIAL REFERENCE TO TWINS

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INTRODUCTION

WHILE the occurrence of right-and left-handedness does not appear to conform to any simple Mendelian formula, the familial incidence of left-handedness rather definitely indicates a genetic basis. Children are more likely to be left-handed if one parent is left-handed, than if both are right-handed (CHAMBERLAIN 1928), and in families where *both* parents are left-handed about 50 percent of the children are also left-handed.

Students of twins generally agree (NEWMAN 1928, LAUTERBACH 1925, WILSON and JONES 1934) in finding a higher percentage of left-handedness in both monozygotic and dizygotic twins than in single born populations. This increase is due principally to the frequent occurrence of intra-pair differences in handedness, rather than to any excess of pairs in which both members are left-handed. Both types of twins differ from the single born in that the conditions *in utero* are necessarily changed. But if the position *in utero* is responsible for the differences in the expression of handedness in certain pairs of twins, why does it not affect *all* twin pairs similarly?

NEWMAN (1928, 1937) is of the opinion that in monozygotic twins, embryonic division occurs near or during gastrulation. As the axis of the embryo and bilateral asymmetry are established during gastrulation, he assumes that monozygotic twins which do not separate until after gastrulation will exhibit intra-pair differences in handedness, whereas those separating before gastrulation will be of the same handedness. He also attributes intra-pair variations in other bilateral asymmetrical traits, such as dermatoglyphics, direction of head hair whorl and dentition to the same cause. But if this is the correct explanation, there should be a definite stage in embryonic development for the establishment of each trait showing bilateral asymmetry, beyond which separation of the embryo should result in intra-pair variation, but if separation should occur at some previous time the members of the pair would be alike. Thus we should expect definite combinations of intra-pair trait reversals in monozygotic twins. For example, we might expect to find some twins showing no intra-pair differences in either handedness or direction of hair whorl, some to show reversals in handedness and the same direction of head hair whorl (assuming handedness normally to be established first), some to show differences in both traits, but none to show reversals in hair whorl and the same handedness. Actually, however, we find all possible combinations in respect not only to handedness and hair whorl, but also to any other traits involving bilateral asymmetries. We might logically expect to find *situs inversus viscerum* in one member of monozygotic twin pairs in a high percentage of cases, but actually such cases are extremely rare. Furthermore, Newman's hypothesis completely fails to account for the excess of left-handedness in dizygotic twins.

LAUTERBACH (1925) offers an alternative explanation in which he states "the causes which operate to produce twins also operate to produce left-handed individuals." Considering the quite different modes of origin of the two types of twins, such a hypothesis seems questionable. If true, however, we might expect a higher percentage of left-handers in the non-twin members of the families of twins, than in non-twin families. Such a comparison is included in this paper.

The writer (1938) has observed an apparently high frequency of left-handers among the relatives of twins showing intra-pair variations in handedness, as contrasted with a low frequency of left-handed relatives of twins where both members are right-handed. These observations have suggested a different hypothesis, which could apply to both monozygotic and dizygotic twins. Handedness is assumed to be a quantitative trait, and those individuals who are genotypically intermediate may easily be shifted one way or another in the determination of manual preference. Unusual position *in utero* is one circumstance which may finally condition the handedness of such individuals. The handedness of individuals genotypically strongly right-handed or strongly left-handed, would not be affected by circumstances *in utero*. Thus monozygotic twins showing intra-pair reversals in handedness are assumedly genotypically intermediate in handedness, and the unusual position *in utero* results in one becoming left-handed and the other right-handed. Members of fraternal twin pairs are, of course, of different genotypes, but here, too, the unusual position *in utero* may be sufficient to condition the handedness of genotypically intermediate individuals. A similar explanation for the increase of left-handedness in twins was given by VERSCHUER (1931, 1932).

If the above hypothesis is correct, we should expect to find a higher incidence of left-handedness among the relatives of pairs containing one right-handed and one left-handed member than among the relatives of pairs where both members are right-handed. In this paper we present an analysis of data of our own, as well as that of various other investigators, on the incidence of left-handedness in both twins and the single born.

THE DIAGNOSIS OF HANDEDNESS

There is no general agreement among students of handedness as to just what constitutes right-handedness or left-handedness. The fact that an association exists between the kicking foot, the dominant eye and the preferred hand has led some investigators (LECHE 1933) to include the kicking foot and the dominant eye among the criteria of handedness. DOWNEY (1927) included both unimanual and bimanual operations in her analyses of handedness. JONES (1918) classified people as to handedness on the basis of arm measurements. NEWMAN (1937) used electrical tapping tests as his criteria for the handedness of twins. Novel tests for handedness, such as blindfolding a person and seeing which way they turn when walking have also been suggested. OJEMANN (1930) in an analysis of artificial tests of handedness such as tapping tests, has shown them to be unreliable. Testimony as to preferred hand, and actual performance appear to be the most reliable tests of handedness. It is hazardous, however, to classify handedness on the performance of only one or two types of tests as has too frequently been done. Writing, for example, is a poor criterion when used alone, in determining the incidence of left-handedness, as so many left-handers have been trained to write with their right hands. When used with other criteria, it is of considerable value, as only rarely do we find right-handers writing with their left hands. Throwing is an excellent criterion for males, but unreliable for females, whereas the hand used for holding a needle is a good criterion for females, and a poor one for males.

In our own classification of handedness, we refer to the hand preferred in the performance of unimanual operations. Our data on an individual's handedness includes his testimony as to whether he considers himself right- or left-handed, or ambidextrous, and the preferred hand for each of the following:[1]

1. Throwing	6. Hammer
2. Bowling	7. Saw
3. Marbles	8. Sewing
4. Knife	9. Writing
5. Spoon	10. Scissors

We have arbitrarily grouped those tested into two classes, right-handers and left-handers. Right-handers include only those who use the right hand for all ten operations, and left-handers those who use the left hand or either hand with equal ease in one or more of the operations.

THE INCIDENCE OF LEFT-HANDEDNESS IN THE GENERAL POPULATION

We recently conducted a survey of the handedness of 687 families. All were families of whom one or more members were students at Ohio State University, taking some course in elementary zoology. Questionnaires

[1] These criteria were suggested by PROF. J. M. RIFE, of Muskingum College.

were prepared asking about the handedness of each member of the family in respect to all items included in our criteria. The students were carefully instructed in the classroom as to how to take the data, and were cautioned not to answer any items concerning which they could not obtain first-hand information. As the questionnaires were given out just before Thanksgiving vacation, the students, with only a few exceptions, had

TABLE 1

The familial occurrence of right- and left-handedness.

TYPE OF CHILDREN	R♂×R♀ (620 MATINGS)	R♂×L♀ (30 MATINGS)	L♂×R♀ (32 MATINGS)	L♂×L♀ (5 MATINGS)
R♂	1084	33	40	2
R♀	758	26	41	3
R♂+♀	1842	59	81	5
L♂	105	6	9	3
L♀	46	10	9	3
L♂+♀	151	16	18	6

opportunities to directly contact the members of their immediate families. Table 1 summarizes the raw data. The excess of males is due to the fact that the great majority of elementary zoology students are males. In a total population of 3542 we find that 263, or 7.45 percent are left-handed. Table 2 shows a close agreement between our findings and those of other investigators.

TABLE 2

Frequencies of left-handedness in the general population.

	NO. OF INDIVIDUALS TESTED	%L
Jones and Wilson	521	6.5
Neall	800	6.5
Quinan	1000	7.6
Rife	3542	7.45

Of the 263 left-handers, 100 are left-handed in all ten operations, and 33 are left-handed in all operations except writing. Twenty-eight are left-handed in only one operation, of whom thirteen are left-handed in throwing, and one is left-handed in writing. No individuals are right-handed only in throwing. Left-handed children occur in families where both parents are right-handed, and five out of a total of eleven children are right-handed in families where both parents are left-handed. These figures indicate the quantitative nature of handedness and clearly show that its inheritance cannot be explained solely on the basis of a single pair of factors.

The fact that left-handed children occur more frequently in families where one or both parents are left-handed is strikingly shown in the 2×2 table (table 3). Here we find $\chi^2=41.7$. As any value of χ^2 beyond 3.841 is considered to be significant, in an analysis involving one degree of freedom, no further comment seems necessary to indicate the tremendous significance of the above differences. It is of interest to remark,

TABLE 3

Two-by-two table showing the incidence of right- and left-handedness among offspring where both parents are right-handed, as contrasted with offspring where one or both parents are left-handed.

	TYPE OF MATING		
	R×R	R×L & L×L	TOTALS
R children	1842	145	1987
L children	151	40	191
Totals	1993	185	2178

$\chi^2=41.7$.

however, that our data include a family of five, of which both parents and all three children are left-handed. The children perform all diagnostic operations left-handed, and the parents are left-handed in all except writing. As only about 50 percent of those classed by us as left-handers are as completely left-handed as members of this family, the frequency of the occurrence of such families, if handedness were purely a matter of chance, should be approximately one in a million families of five ($.04^5$).

HANDEDNESS OF TWINS

Numerous investigators have collected data on the incidence of left-handedness in twins. Unfortunately, there has been little uniformity as to criteria used, and some investigators even fail to state any. The writer has obtained data on the handedness of 223 monozygotic and 146 dizygotic pairs of twins. Each pair was tested by the writer and his assistants.

TABLE 4

The frequencies of R-R, R-L and L-L pairs in monozygotic and dizygotic twins.

	MONOZYGOTIC								DIZYGOTIC							
	R-R		R-L		L-L				R-R		R-L		L-L			
	NO.	%	NO.	%	NO.	%	TOTAL	% OF L INDIVIDUALS	NO.	%	NO.	%	NO.	%	TOTAL	% OF L INDIVIDUALS
NEWMAN	30	60	17	34	3	6	50	23	39	78	11	22	0	0	50	11
WILSON & JONES	56	80	13	18.6	1	1.4	70	10.7	97	88.9	24	19.5	2	1.6	123	11.4
RIFE	176	79.5	41	18.3	6	2.2	223	11.35	104	71.3	39	26.7	3	2	146	15.35
Totals	**262**	**76.0**	**71**	**20.7**	**10**	**3.4**	**343**	**14.0**	**240**	**75.3**	**74**	**23.2**	**5**	**1.5**	**319**	**13.1**

Table 4 is a summary of the data obtained by three American investigators. WILSON and JONES (1934) used throwing and writing as their criteria for handedness. NEWMAN (1937) used tapping tests and testimony as diagnostic criteria. WILSON and JONES' data on monozygotic twins agree closely with our own whereas NEWMAN finds a significantly greater frequency of left-handers in this group. Among dizygotic twins we encountered a higher frequency of left-handedness than did either NEWMAN, or WILSON and JONES. None of the differences in this latter group, however, are statistically significant. All three investigators agree in finding significantly higher percentages of left-handedness in both types of twins than the 7.45 percent obtained in our group of single born individuals.

Table 5 shows the relative frequencies of R-R, R-L and L-L sib pairs in our group of single born individuals, as contrasted with similar groupings for both types of twins. It is apparent that the higher incidence of left-handedness in twins is due principally to the relatively high frequencies of R-L pairs.

TABLE 5

Comparative frequencies of R-R, R-L and L-L pairs in monozygotic twins, dizygotic twins and paired sibs.

	R-R		R-L		L-L	
	No.	%	No.	%	No.	%
Monozygotic	262	76	71	20.7	10	3.4
Dizygotic	240	75.3	74	23.2	5	1.5
Sibs	3067	85.6	475	13.2	41	1.2

THE INCIDENCE OF LEFT-HANDEDNESS IN THE IMMEDIATE FAMILIES OF TWINS

Table 6 summarizes in two-by-two tables our data in regard to the handedness of the immediate relatives of twins. By immediate relatives we refer to parents and sibs. For the identical twins $\chi^2 = 12.8$ and for the fraternal $\chi^2 = 18.1+$. Such values show conclusively that left-handedness occurs more frequently among the immediate relatives of R-L twins, than among the relatives of R-R twins. This is in harmony with what we might expect, if R-L twins are genotypically intermediate in handedness.

Table 7 shows data in two-by-two tables pertaining to the relative frequencies of left-handedness of the single-born in families containing twins, and those containing no twins. Table 7A shows that the incidence of left-handedness is significantly less in the immediate relatives of monozygotic twins, than in non-twin families. This is just the reverse of what we might expect if the same factors are responsible for left-handedness and twinning, as assumed by LAUTERBACH (1925). We are at a loss, however, to explain why left-handedness should occur with significantly *lower* frequency among the relatives of monozygotic twins. Table 7C shows no significant differences between non-twin families and the families of dizygotic twins in regard to the incidence of left-handedness. Also, when the twins are included, as shown in tables 7B and D, there is no significant

TABLE 6

Two-by-two tables showing the comparative frequencies of left-handed relatives for R-R and R-L twins.

MONOZYGOTIC TWINS

	R-R	R-L	TOTAL
Without L relatives	105	25	130
With L relatives	26	22	48
Total	131	47	178

$\chi^2 = 12.8$

DIZYGOTIC TWINS

	R-R	R-L	TOTAL
Without L relatives	84	12	96
With L relatives	16	15	31
Total	100	27	127

$\chi^2 = 18.1+$

difference in the frequency of left-handedness in non-twin and twin bearing families. These data are apparently not in accord with LAUTERBACH'S explanation of the greater frequency of left-handedness among twins.

SUMMARY

While our criteria for handedness are by no means perfect, and our classification of left-handers is somewhat arbitrary, the data conclusively indicate the following points. Left-handers are more likely to have left-handed children than are right-handers. The inheritance of left-handedness cannot be explained solely on the basis of a single pair of genetic factors. There is considerable evidence that handedness is a graded or quantitative trait. Left-handedness occurs more frequently in both monozygotic and dizygotic twins than in the single born, this being due to the relatively frequent occurrence of pairs of whom one member is right-handed and the other left-handed. In both monozygotic and dizygotic twins, pairs in which one member is left-handed have a significantly higher percentage of left-

handed relatives than do pairs composed only of right-handers. Twin bearing families show no greater incidence of left-handedness than do non-twin bearing families.

The following hypothesis may account for the excess of left-handers among twins. As handedness is a quantitative trait, many individuals are genotypically intermediate, that is, not strongly biased in either direction.

TABLE 7*

Two-by-two tables showing comparative frequencies of left- and right-handedness in twin bearing and non-twin bearing families.

	NON-TWIN FAMILIES	FAMILIES OF IDENTICAL TWINS	TOTALS
Right-handed	3279	978	4257
Left-handed	263	56	319
Totals	**3542**	**1034**	**4576**
	A		
	$\chi^2 = 4.9$		

	NON-TWIN FAMILIES	FAMILIES OF IDENTICAL TWINS	TOTALS
Right-handed	3279	1128	4407
Left-handed	263	98	361
Totals	**3542**	**1226**	**4768**
	B		
	$\chi^2 = .42$		

	NON-TWIN FAMILIES	FAMILIES OF FRATERNAL TWINS	TOTALS
Right-handed	3279	509	3788
Left-handed	263	34	297
Totals	**3542**	**543**	**4085**
	C		
	$\chi^2 = .90$		

	NON-TWIN FAMILIES	FAMILIES OF FRATERNAL TWINS	TOTALS
Right-handed	3279	716	3995
Left-handed	263	63	326
Totals	**3542**	**779**	**4321**
	D		
	$\chi^2 = .40$		

* In tables A and C, the twins are not included. In B, R-R pairs are included as right-handed individuals and R-L and L-L pairs as left-handed individuals. In D, R-R pairs are included as two right-handed individuals, L-L pairs as two left-handed individuals, and R-L pairs as having one right-hander and one left-hander.

The handedness of such individuals can easily be shifted one way or the other by environmental conditions. In twins, intra-uterine circumstances, such as position and crowding may condition the handedness of such individuals, resulting in one being left-handed and the other right-handed. Individuals genotypically strongly biased for either right- or left-handedness, would not be shifted by environmental circumstances. Thus identical twins genotypically strongly right-handed or left-handed show no intra-pair differences in handedness. Fraternal twins, having different genotypes, may show intra-pair differences in handedness, both on account of different genotypes and on account of the environmental conditioning of genotypically intermediate individuals. We should expect more left-handedness among the relatives of genotypically intermediate twins than among the relatives of genotypic right-handers. Our data are in harmony with the above conditions.

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